BRACHIAL PLATE STRUCTURE IN THE BRACHIOPOD FAMILY PENTAMERIDAE

by THOMAS W. AMSDEN

ABSTRACT. The pentameracean family Pentameridae is characterized by long, rod-like or blade-like brachial processes, buttressed at their posterior end by high plates extending forward far enough to enclose the brachial muscle field. Variations in the internal structure of the brachial valve, combined with changes in external form of the shell, permit the family to be divided into three subfamilies: Pentamerinae, Gypidulinae, and Clorindinae. The articulating muscles in the pedicle valve were seated in the trough-like spondylium which has remained relatively stable and unchanged throughout the history of the family. The Pentameridae range from the Late Ordovician into the Late Devonian.

A new genus *Clorindella*, type species *C. areyi*, is proposed for costate Clorindinae with a brachial cruralium. The genus *Pentameroides* Schuchert and Cooper, 1931, is redescribed and the subfamily *Pentameroidinae* Amsden, 1953, is abandoned. *Pentamerella* Hall, 1867, is redescribed on the basis of Hall's type specimens of *P. arata*. Additional information is furnished on the internal structure of *Conchidium munsteri* St. Joseph, 1938, based on topotype material from Zone 5b of Norway.

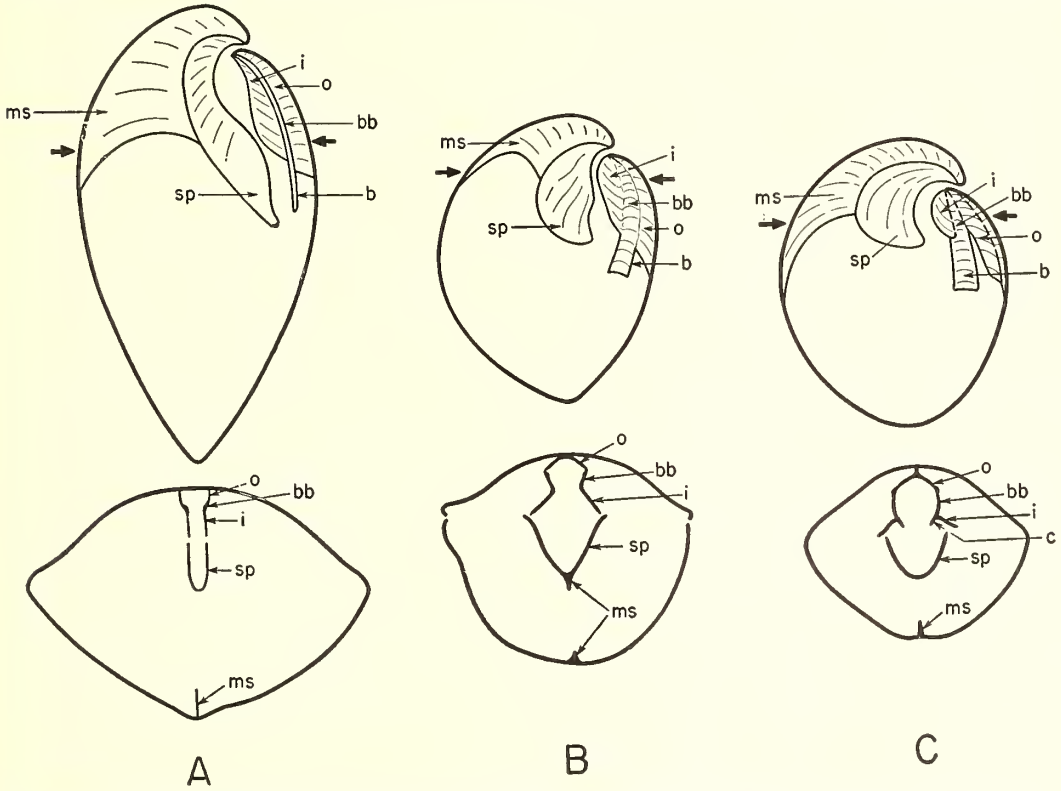
THE writer has been studying the brachiopod superfamily Pentameracea in preparation for the forthcoming *Treatise on Invertebrate Paleontology*. A number of genera representing the family Pentameridae have been restudied by means of serial sections. Some of the shells sectioned are extremely well preserved and an examination of these thin sections and parlodion peels, as well as some etched material, indicates the need for some revision in previously recognized taxa, and the introduction of a new genus, *Clorindella*.

The terminology herein applied to the plate structure of the brachial valve is essentially the same as that employed by Schuchert and Cooper (1932, pp. 162–5), and by the writer in 1953 (pp. 137–40), and is illustrated by means of labelled photomicrographs (Pls. 40 to 43), and by line drawing (text-fig. 1). The cardinalia of the Pentameracea consists of fairly long, rod-like or blade-like *brachial processes* supported at their posterior end on plates of various lengths. This apparatus attains its strongest development in the Pentameridae where its basic structure may be referred to three sets of plates: *outer plates*, *brachial processes*, and *inner plates*. The outer plates rest directly on the floor of the valve and may be parallel and discrete, or they may unite to produce a cruralium. The inner plates are subparallel at their forward ends, but towards the posterior they curve outward to meet the lateral walls of the valve. The sockets are excavated out of the posterolateral parts of the inner plates (Pl. 40, fig. 6), and the entire apparatus thus served to buttress the articulating mechanism and to strengthen the lophophore supports.

The morphology of the pedicle valve is relatively stable and is treated only briefly in this report. All pentameraceans have a well-developed spondylium, which served as the seat of attachment for the principal muscles. The spondylium is generally supported on a median septum for at least a part of its length (Pl. 40, figs. 1, 2, 4, 7, 8; text-fig. 1). Kozlowski (1929, p. 124, fig. 38) called this a spondylium duplex and thought that the supporting septum was formed by the two walls of the spondylium being brought into contact. According to Kozlowski the septum in transverse section appeared to be com-

[Palaeontology, Vol. 7, Part 2, 1964, pp. 220–39, pls. 40–43]

posed of two layers separated by a well-defined line of junction. This interpretation has been accepted by many subsequent investigators, but, in a recent study of *Enantiosphen vicaryi*, Williams and Wright (1961, pp. 164–5, text-fig. 8) presented evidence to show that the supporting septum, at least in this species, was composed of a thin median layer,

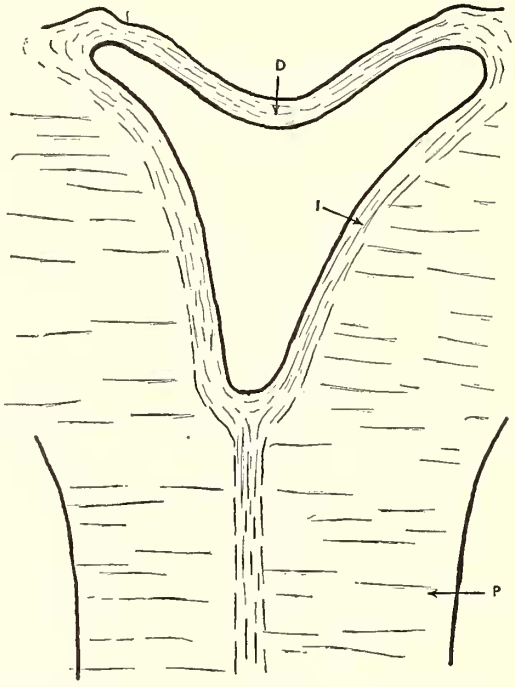


TEXT-FIG. 1. Longitudinal (above) and transverse (below) sections showing the internal structure of the three subfamilies of the Pentameridae. Heavy, unlettered arrows on longitudinal sections show position of transverse sections. A, Subfamily Pentamerinae. *Pentamerus* cf. *P. oblongus* Sowerby, Reynales Limestone, Rochester, N.Y.; photomicrographs of this species on Plate 40, fig. 4, and Plate 42, figs. 1, 2. B, Subfamily Gypidulinae. *Sieberella roemeri* Hall and Clarke, Henryhouse Formation, Pontotoc Co., Okla.; photomicrographs of this species on Plate 43. C, Subfamily Clorindinae. *Cloriudella areyi* (Hall and Clarke), Irondequoit Limestone, Rochester, N.Y.; photomicrographs of this species on Plate 42, figs. 3–5.

b—brachial process; bb—posterior extension of brachial process; c—carinae; i—inner plate; ms—median septum; o—outer plate; sp—spondylium.

in part discontinuous, lined on both sides with a thicker layer of secondary calcite. Thin sections of other species studied by the writer appear to support Williams and Wright's interpretation. The thin section of *Sieberella roemeri* (Pl. 40, figs. 1, 2), shows that the spondylium and supporting septum are composed of a thin median layer which is coated on both sides with a thicker layer of shell material, the latter presumably representing the outer part of the secondary layers (compare with text-fig. 8C of Williams and

Wright). This basic shell structure is especially well shown in thin sections and parlodion peels of *Pentamerus* cf. *P. oblongus* from the Reynales Limestone (Pl. 40, fig. 4; text-fig. 2). At suitably high magnifications the median septum of this species may be seen to be composed of a thin median layer, and a fairly thick, outer prismatic layer of clear calcite. The inner layer can be followed from the central part of the septum into the spondylium and the deltidium (text-fig. 2). This is similar to the relationship observed by Alexander (1948, p. 147, fig. 3) on *Conchidium knighti*, where she recognized three shell layers: an



TEXT-FIG. 2. *Pentamerus* cf. *P. oblongus* Sowerby. Transverse section of a part of the spondylium and the deltidium showing the shell layers. This is an enlarged drawing of the photomicrograph shown in Plate 40, fig. 4.

D—deltidium; P—prismatic layer; S—inner layer.

outer layer, an inner layer, and a thick prismatic layer. In the specimens studied by the writer the distinction between the inner shell layer and the prismatic layer is obscure, and supports the conclusion of Williams (1956, pp. 249–51) that the prismatic layer is simply a modification of the inner secondary layer. This layer is thick at the posterior end of the shell, and thins markedly towards the front. The prismatic layer is well displayed on the specimen of *Pentameroides sp.* (Pl. 41, figs. 6–12); at the posterior end of the brachial valve it almost completely buries the brachial apparatus (Pl. 41, fig. 6), but thins sharply towards the front (Pl. 41, fig. 10).

A deltidium has been observed on species of *Pentamerus* (Pl. 40, fig. 4), *Conchidium*, *Aliconchidium*, and *Enantiosphen*, and, since it is a thin, delicate structure which would be easily destroyed, it may be more commonly developed than present knowledge indicates.

The different pentameracean genera show some variation in the length of the spondylium and in the development of the supporting septum. In some genera, such as *Holorhynchus* and *Cymbidium*, the septum is absent and the spondylium is attached directly to the valve floor; in other genera such as *Harpidium* (Pl. 40, fig. 8) it is relatively short whereas in still others it is much longer, reaching an extreme in such genera as *Brooksina* (Pl. 40, fig. 7) where it almost divides the interior of the shell into two parts. Aside from these modifications the spondylium was a conservative structure, exhibiting little phylogenetic variation throughout the history of the Pentameracea, and consequently the morphology of the pedicle valve has not been used in classification above the generic level.

Sapelnikov (1963, p. 65) proposed a new subfamily, Subrianinae, for those Pentameridae without any supporting median septum in the pedicle valve; this subfamily included three genera: *Holorhynchus* Kiaer, 1902, *Cymbidium* Kirk, 1926, *Subriana* (*Subriana*) Sapelnikov, 1960, and *Subriana* (*Vagranella*) Sapelnikov, 1960. As noted above, the length of the median septum is variable and in the writer's opinion does not constitute a valid distinction for a new subfamily. *Holorhynchus* Kiaer, 1902 is here assigned to the family Virgianidae and *Cymbidium* Kirk, 1926 is assigned to the family Pentameridae, subfamily Pentamerinae; the writer has not seen Sapelnikov's description of *Subriana* (*Subriana*) and *Subriana* (*Vagranella*).

The Pentameracea comprise the following five (four?) families of middle Palaeozoic brachiopods: [?] Parallelelasmatidae Cooper, 1956; Stricklandiidae Hall and Clarke, 1894 (emended Boucot and Ehlers, 1963); Virgianidae Boucot and Amsden, 1963; Enantiosphenidae Torley, 1934; Pentameridae McCoy, 1844. All of these brachiopods have a pedicle spondylium, usually resting on a median septum, and fairly long brachial processes, which supported at least a part of the lophophore. The brachial processes are free at their distal ends, except in the family Enantiosphenidae where they terminate in a loop. The processes are supported at their posterior ends by plates which, in the families Pentameridae, Parallelelasmatidae, and Enantiosphenidae, extend forward far enough to enclose the muscle field, but which, in the Virgianidae and Stricklandiidae, are so abbreviated that they exclude the area of muscle attachment. The Parallelelasmatidae include a small group of Middle Ordovician brachiopods the inclusion of which within the Pentameracea has recently been questioned by Williams (1962, pp. 231–2). With the exception of this family, which the author provisionally retains within the superfamily, the Pentameracea range from the Late Ordovician (Ashgillian) to the Late Devonian, being fairly abundant in the shelly faunas of the Silurian and Early Devonian. Almost all of the Late Ordovician (Ashgillian) and Early Silurian (early and middle Llandoverian) pentameraceans have abbreviated supports for the brachial processes. This group comprises the Virgianidae, which are believed to be confined to the Late Ordovician (Ashgillian) and Early Silurian (Llandoverian), and the Stricklandiidae which appear to be confined to the Lower and Middle Silurian. Recently Nikiforova (1960, p. 202) and Rzhonsnitskaya (1961, p. 39) have proposed to remove the Stricklandiidae from the Pentameracea and place them in the Camerellacea (these authors include *Virgiana* and *Holorhynchus* in the Pentameridae). This group of shells are, however, essentially pentameracean in all respects except for their abbreviated plates, and are believed to be more closely related to the Pentameridae than to the Camerellidae. Nikiforova (1960, p. 211) also removed the Enantiosphenidae from the Pentameracea, referring this family

with question to the Terebratulida. The sole representative of this family is the Middle Devonian genus *Enantiosphen*, which has a typically pentameracean pedicle and brachial internal structure, except for the fact that the processes terminate in a loop (Amsden, 1953, p. 138; Williams and Wright, 1961, p. 164; Cloud, 1942, pp. 144–5). Furthermore, this genus has an impunctate, fibrous shell like that of the Pentameracea, and quite unlike the punctate shell of the Terebratulacea.

Family PENTAMERIDAE M'Coy 1844

This family includes smooth, costate, granulose, or pitted shells with or without interareas. Generally the shells are strongly biconvex. The brachial processes are supported by well-developed inner and outer plates, the latter extending forward far enough to enclose the muscle area. In some genera the outer plates are parallel and discrete, and in others they unite to form a cruralium. The processes are long, rod-shaped or blade-shaped structures with free distal ends. The pedicle valve has a well-developed spondylium, commonly supported on a median septum.

This is the only family of Pentameraceans discussed in the present paper. They are fairly common in the shelly faunas of the late Lower Silurian to Lower Devonian, but range on into the Late Devonian. A single species, *Conchidium munsteri*, is present in Late Ordovician (Ashgillian) strata of Norway. The stratigraphic position of this species is somewhat anomalous because, according to present information, the next younger representative of the Pentameridae does not appear until the latter part of the Lower Silurian; the internal morphology and age of *C. munsteri* is discussed below.

Three subfamilies are here included in the Pentameridae:

Pentamerinae M'Coy 1883
Gypidulinae Schuchert and Levene 1929
Clorindinae Rzhonsnitskaya 1956

In a recent paper Nikiforova (1960, pp. 203–5) divided this group of pentameraceans into four families: Pentameridae, Gypidulinidae, Pentameroidinae Amsden, 1953, and a new family, the Antirhynchonellidae. Nikiforova's diagnosis of Pentameroididae was the same as that given by Amsden in 1953, and the family Pentameridae is essentially the same as the present subfamily Pentamerinae except for the inclusion of *Virgiana* and *Holorhynchus* (these two genera have abbreviated brachial plates and are assigned to the Virgianidae). According to Nikiforova, both the Antirhynchonellidae and Gypidulidae possess a fold and sulcus, the latter having discrete outer plates and the Antirhynchonellidae having the plates united to produce a cruralium.

Rzhonsnitskaya (1961, pp. 42–44) uses a somewhat different classification, recognizing the following families and subfamilies:

Family Pentameridae
  Subfamily Pentamerinae
  Subfamily? Pentameroidinae
  Subfamily Conchidiellinae, new subfamily
Family Gypidulidae
Family Clorindidae

According to Rzhonsnitskaya, the Pentameridae either lack a fold and sulcus or have this structure only weakly developed, and possess long, stalk-like processes. The sub-

family Pentamerinae was defined as including forms having a tripartite brachial apparatus and long, thin processes. Rzhonsnitskaya's diagnosis of this subfamily is similar to the writer's, except that it includes *Virgiana* and *Holorhynchus* (here assigned to the Virgianidae). The Pentameroidinae was accepted, with question, as defined by the writer. A new subfamily, the Conchidiellinae, was proposed for pentamerids with a tripartite brachial apparatus and massive, convex processes. Three genera were included in this subfamily: *Conchidiella* Khodalevich, 1939; *Zdimir* Barrande, 1881; and *Leviconchidiella* Rzhonsnitskaya, 1960. In a forthcoming restudy of Barrande's genus *Zdimir*, Boucot and Siehl (1962) propose to supress *Conchidiella* as a synonym of *Zdimir*, and refer *Zdimir* and *Leviconchidiella* to the Gypidulinae. According to these authors, these genera have brachial-plate structures basically the same as *Gypidula* and other members of this subfamily. Rzhonsnitskaya restricted the Gypidulidae to those pentamerids with a ventral fold and dorsal sulcus, and massive, stalk-like processes. The Clorindidae were characterized as having a ventral sulcus and a dorsal fold, and a carinate brachial apparatus. These families include about the same genera as they do in the present study (as subfamilies), the principal exception being *Pentamerella* which Rzhonsnitskaya placed in the Clorindidae and which the writer places in the Gypidulinae (see description of *Pentamerella arata*). Also it should be kept in mind that the Gypidulinae of the present work includes genera which Rzhonsnitskaya referred to the Conchidiellinae.

Subfamily PENTAMERINAE Waagen 1883

This group includes smooth, costate or costellate brachiopods, most of which have poorly developed interareas. The shells tend to be larger than most middle Paleozoic brachiopods and some species, such as *Conchidium alaskense* Kirk and Amsden and *C. vogulicum* (Verneuil), are among the largest known brachiopods. They generally lack a fold and sulcus, or if these are present they are poorly developed. The brachial apparatus is tripartite, consisting of inner plates, outer plates, and relatively long, rod-like brachial processes (text-fig. 1A). These plate divisions are commonly clearly marked, both in transverse section (Pl. 42, figs. 1, 2) and in shells split longitudinally to expose one of the brachial plates (Pl. 40, figs. 7, 8). All the genera assigned to this subfamily have discrete outer plates, except for *Pentameroides* in which outer plates are united to form a median septum (the brachial interior of *Pleurodium* is unknown).

The internal structure of *Pentamerus* is quite characteristic of this group of pentamerids (text-fig. 1A; Pl. 40, fig. 4; Pl. 42, figs. 1, 2). The processes are slender rods which served to support at least part of the lophophore. These are supported on long, parallel outer plates which remain discrete throughout their length. The inner plates are well developed, although not quite as long as the outer plates; near their anterior end they are subparallel, but towards the rear they curve outward to meet the lateral walls of the valve, where they form a part of the articulating mechanism.

Shell growth is believed to have taken place in the following manner. In young, immature shells the brachial apparatus was small and confined to the posterior end of the valve. At this stage the apparatus resembled a mature representative of the Stricklandiidae or Virgianidae. As the shell grew larger the inner and outer plates were extended forward, encroaching upon and covering the proximal ends of the brachial processes. To strengthen this part of the shell additional material was deposited over the entire

apparatus (and spondylium), thus to some extent burying the posterior part of the brachial processes (Pl. 41, figs. 6, 7, 12; Pl. 42, figs. 1, 2). Even so, the processes are generally clearly marked in thin sections and parlodion peels of well-preserved specimens.

In 1954 the International Commission on Zoological Nomenclature placed *Pentamerus* Sowerby, 1813 (type species *Pentamerus oblongus* Sowerby, 1813) and *Conchidium* Oehlert, 1887 (type species *Anomia bilocularis* Hisinger, 1799) on the *Official List of Generic Names in Zoology*.

The following genera are now assigned to the Pentamerinae: *Pentamerus* Sowerby, 1813; *Brooksina* Kirk, 1922; *Capelliniella* Strand, 1928; *Conchidium* Oehlert, 1887; *Cymbidium* Kirk, 1926; *Harpidium* Kirk, 1925; *Lissocoelina* Schuchert and Cooper, 1931; *Pentameroides* Schuchert and Cooper, 1931 (see below); *Rhipidium* Schuchert and Cooper, 1931. *Pleurodium* Wang, 1955, is provisionally included in this subfamily although the internal structure of the brachial valve is unknown. *Pentamerifera* Khodalevich, 1939, is also assigned questionably to this subfamily, although its internal structure is not clear to the writer. *Aliconchidium* St. Joseph, 1942, may also be appended to the Pentamerinae; however, it differs markedly from the other genera in having a prominent pedicle palintrope. Recently Sapelnikov (1960, pp. 56–62, pls. 5, 6, text-figs. 1–3) described a new genus of Pentameridae, *Jolvia*, which is unusual in having a cardinal process; Sapelnikov's photographs (pl. 6, figs. 5, 6) suggest that this structure is

---

EXPLANATION OF PLATE 40

Figs. 1, 2. *Sieberella roemeri* Hall and Clarke, 1892. Henryhouse Formation, Pontotoc Co., Okla. 1, Photomicrograph of a thin section showing the complete spondylium and supporting septum (×15). 2, Enlarged detail of the same (×75). Okla. Univ. 5173.

Fig. 3. *Conchidium munsteri* St. Joseph, 1938. Late Ordovician (zone 5b), Vestre Svartoy, Ringerike, Norway. Parlodion peel showing brachial-plate structure (×10). See text-fig. 4(3). Paleont. Mus., Oslo, 16668A.

Fig. 4. *Pentamerus* cf. *P. Oblongus* Sowerby, 1813. Reynales Limestone, near Rochester, N.Y. Photomicrograph of a thin section showing part of spondylium and supporting septum and deltidium (×10). Cut near posterior end of valve where spondylium and septum are much thickened by secondary shell material. See text-fig. 2. Okla. Univ. 5174.

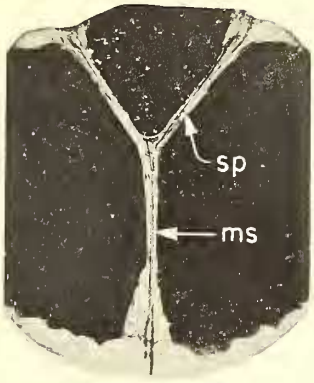
Figs. 5, 6. *Gypidula coeymanensis* Schuchert, 1913. Helderberg Formation, Indian Ladder, Thatcher Park, south of Albany, N.Y. Oblique and vertical views of a silicified valve showing brachial apparatus (×3). Okla. Univ. 5175.

Fig. 7. *Brooksina alaskensis* Kirk, 1922. Upper Silurian, Kosciusko Island, south-eastern Alaska. Specimen split longitudinally to show the ventral spondylium (left) and brachial apparatus (right) (×1½). U.S. Nat. Mus. 142774.

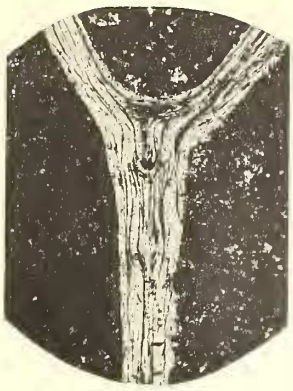
Fig. 8. *Harpidium insignis* Kirk, 1925. Upper Silurian, Kosciusko Island, south-eastern Alaska. Specimen split longitudinally to show ventral spondylium (right) and brachial apparatus (left) (×1). U.S. Nat. Mus. 142775.

Figs. 9–15. *Pentamerella arata* (Conrad), 1841. Specimens figured by Hall, 1867, *Paleont. N.Y.*, vol. 4, pl. 58, figs. 2–4, 13–17. 9, Silicified dorsal interior (×3) 'Upper Helderberg Limestone' (Onondaga Limestone), Albany Co., N.Y. 10, 11, 15, Ventral, dorsal, and anterior views (×1), 'Upper Helderberg Limestone' (Onondaga Limestone), Schoharie Co., N.Y. 12–14, Dorsal, anterior, and ventral views (×2), Schoharie Formation, Schoharie Co., N.Y. All these specimens are at the Am. Mus. Nat. Hist., 2837/4; 2837/3; 2837/2a.

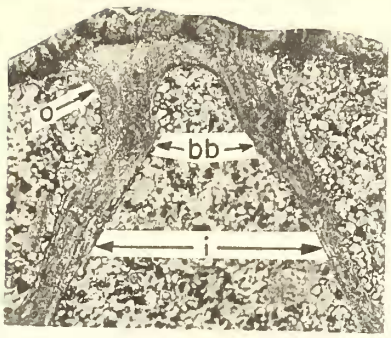
b—brachial process; bb—posterior extension of brachial process; d—deltidium; i—inner plate; ms—median septum; o—outer plate; sp—spondylium.



1



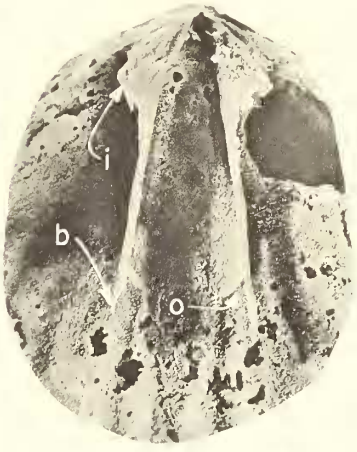
2



3

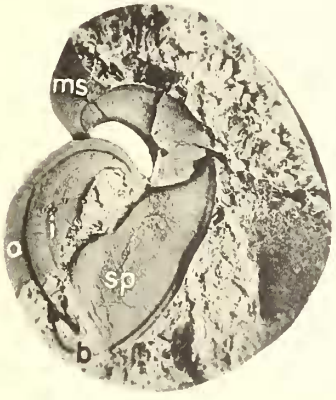
4

5



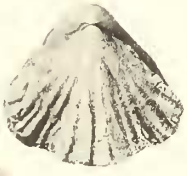
6

7



8

9



10

11

12

13

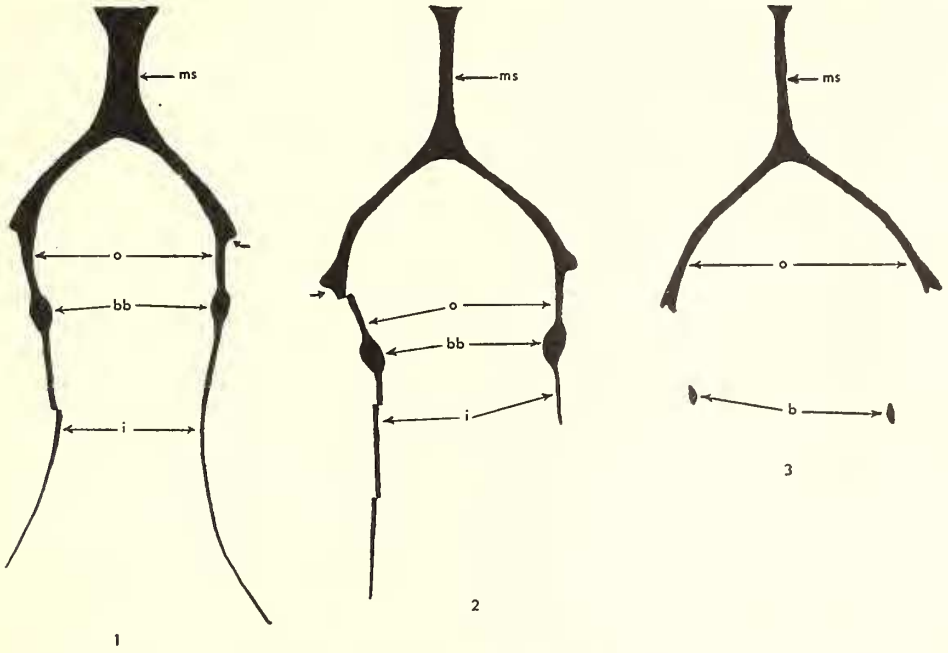
14

15

AMSDEN, Pentameridae

composed of the secondary fibrous layer. *Subriana* Sapelnikov, 1960, may belong here; the writer has not seen the diagnosis of this genus.

With the exception of a single Late Ordovician species, *Conchidium munsteri*, which is discussed below, the subfamily Pentamerinae appears to be restricted to strata ranging in age from late Lower Silurian to Lower Devonian.



TEXT-FIG. 3. Serial sections of the brachial apparatus of *Pentameroides subrectus* (Hall and Clarke), Niagaran, Jones Co., Iowa. These drawings were made from photomicrographs of thin sections; a photomicrograph of number 1 is shown on Plate 41, fig. 2. The small arrows at the sides of numbers 1 and 2 indicate the position at which the outer plates thin abruptly, presumably due to the termination of the thick, secondary layer (specimen is silicified). Distance from posterior tip of ventral beak: 1: 13·5 mm.; 2: 16·8 mm.; 3: 18·8 mm. Thin sections are at the U.S. National Museum.

b—brachial process; bb—posterior extension of brachial process; i—inner plate; ms—median septum; o—outer plate.

Genus PENTAMEROIDES Schuchert and Cooper 1931

Plate 41, figs. 1–12; text-fig. 3

Pentameroides Schuchert and Cooper, 1931, p. 248; 1932, p. 179, pl. 27, figs. 13, 14, pl. 28, figs. 19, 22, text-fig. 27; Amsden, 1953, pp. 144–6, text-fig. 7.

Type species. Pentamerus oblongus subrectus Hall and Clarke 1894, p. 238, pl. 69, figs. 2, 3, 8–10.

Description. Smooth, elongate, moderately to strongly biconvex shells. The pedicle beak is fairly prominent and hooked over, but not in conjunction with the brachial valve (Pl. 41, figs. 3–5, 11). The pedicle valve bears a long, narrow, and deep spondylium supported on a high septum (Amsden, 1953, fig. 7). The brachial apparatus is tripartite, consisting of rod-shaped brachial processes which are braced at their posterior ends by

inner and outer plates. The outer plates are subparallel for a short distance near their junction with the processes, and then converge to produce a cruralium supported on a median septum. The inner plates are thin and very high (Pl. 41, figs. 1, 2; text-fig. 3). Both the inner and outer plates are long, extending forward for more than half the length of the valve (Pl. 41, figs. 3; Amsden, 1953, fig. 7).

Discussion. The present diagnosis is based on a study of topotypes of *Pentameroides subrectus* from the Niagaran strata, Jones County, Iowa, which were borrowed from the U.S. National Museum and from Peabody Museum, Yale University. Thin sections have been prepared from two of these specimens; these are illustrated by photomicrographs on Plate 41, and by line drawings in text-fig. 3. The internal structures of the specimens sectioned have been replaced by silica, so that the microscopic shell structure is obscure. The writer has also prepared serial sections of specimens of *Pentameroides sp.* from the Merritton Member of the Reynales Limestone near Thorold, Ontario. These specimens are not silicified and the detailed shell structure is well preserved as shown in the photomicrographs on Plate 41. The Reynales specimens are congeneric with *P. subrectus*, although they appear to represent a different species.

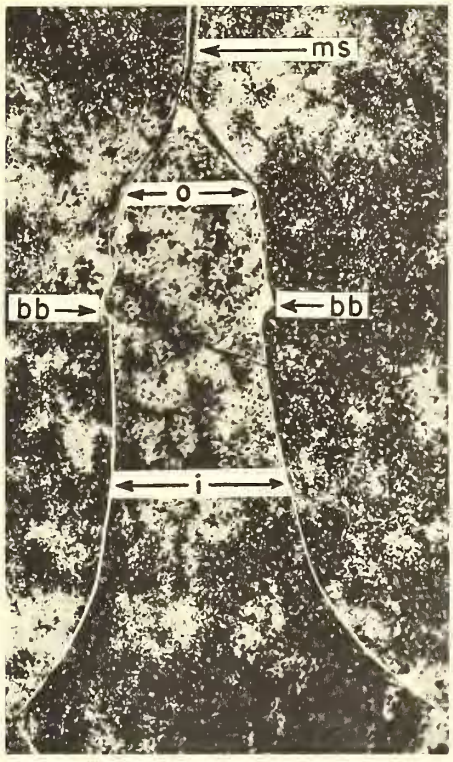
Schuchert and Cooper erected this genus for shells which were externally like *Pentamerus*, but which had a dorsal cruralium. In 1953 the writer redefined this genus and made it the type for a new subfamily, the Pentameroidinae. The genus and new subfamily were thought to be characterized by a fourfold brachial apparatus: inner plates, brachial processes, and outer plates, the latter resting on a fourth set of plates, the septal plates. This diagnosis was based on sections of a topotype of *P. subrectus* from Jones County, Iowa. In this specimen (Pl. 41, fig. 2; text-fig. 3; see also Amsden, 1953, fig. 7) the outer plates thin abruptly at a point about midway between the brachial processes and the median septum. This marked change in thickness was interpreted by the writer as indicating the presence of a fourth element in the brachial apparatus, and was the basis for a new subfamily. This interpretation is now believed to be incorrect. In 1963 a second topotype of *P. subrectus* was sectioned (Pl. 41, fig. 1) and it does not show any trace of this structure, nor does it have any indication of a fourth set of plates. Moreover, serial sections of specimens of *Pentameroides sp.* from Ontario, which appear to have the same internal structure as *P. subrectus* and which are not silicified, give no indication of a fourth plate. These do, however, show that secondary shell material was

EXPLANATION OF PLATE 41

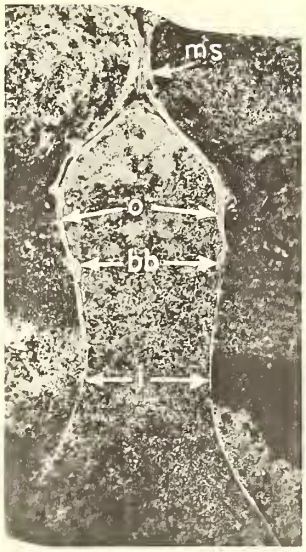
Figs. 1–5. *Pentameroides subrectus* (Hall and Clarke), 1894. Niagaran, Jones Co., Iowa. 1, Photomicrograph of a thin section showing the brachial apparatus approximately 7 mm. in front of the ventral beak (×20); Peabody Mus., Yale Univ., S-1850. 2, Photomicrograph of a thin section of the brachial apparatus (see text-fig. 3) about 13·5 mm. in front of the ventral beak (×10); U.S. Nat. Mus. 14776. 3–5, Dorsal, ventral, and posterior views of a steinkern (×1); Peabody Mus., Yale Univ., S-1850.

Figs. 6–12. *Pentameroides sp.* Reynales Limestone, Merritton Member, Thorold, Ontario. 6–9, Serial sections (6, 7, 8 are parlodion peels, 9 is a thin section) of the brachial apparatus (fig. 6 includes ventral spondylium) (×6). 10, 12, Enlarged views (×24) of the sections shown in figs. 8, 9. Distance from ventral beak: fig. 6: 2·7 mm.; fig. 7: 4·2 mm.; fig. 8: 7·3 mm.; fig. 9: 12·9 mm. Okla. Univ. 5176. 11, Dorsal view (×1); Okla. Univ. 5177.

bb—posterior extension of brachial process; i—inner plate; ms—median septum; o—outer plate; sp—spondylium.



1

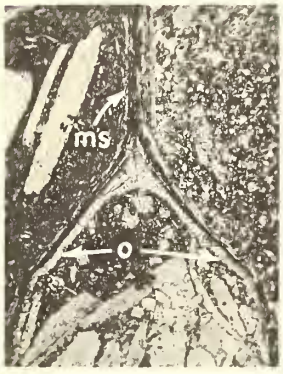


2

3

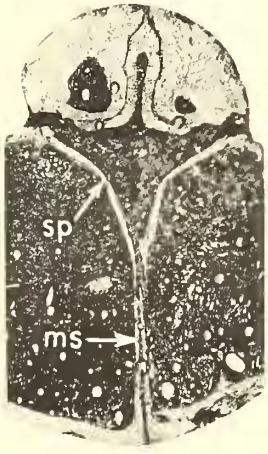
4

5



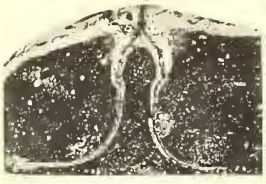
10

11



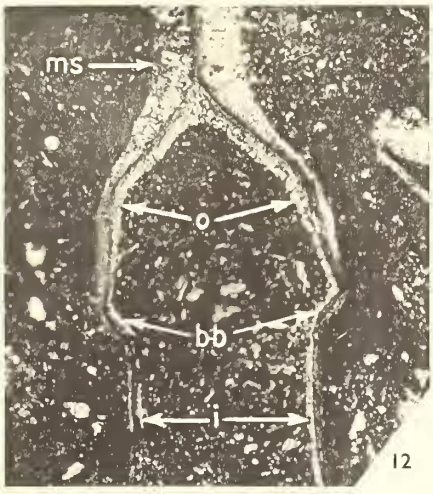
6

8



7

9



12

deposited over the posterior part of the brachial apparatus (Pl. 41, figs. 6–10, 12). In all probability the abrupt thinning of the outer plates shown by the first specimen (Pl. 41, fig. 2; text-fig. 3) is the result of a thinning of the secondary material, somewhat more abruptly than is common, with these relations being obscured by later silicification which destroyed most of the wall structure. *Pentameroides* thus differs from *Pentamerus* only in the presence of a cruralium supported on a septum, and, while this is a sound generic distinction, it is not a suitable subfamilial distinction. Accordingly, it is here proposed that the subfamily Pentameroidinae Amsden, 1953 be abandoned.

This genus includes the type species, *P. subrectus*, *Pentameroides sp.* from the Reynales Limestone at Thorold, Ontario, and *Pentameroides* cf. *P. gothlandicus* (Lebedev; see St. Joseph, 1938, pp. 286–90, pl. v, figs. 7–8, pl. vi, figs. 13, 15, text-figs. 1, 8) from zones 7b and 7c of southern Norway. These are the only species of *Pentameroides* definitely known to the writer, although an investigation of the internal structure of species now referred to *Pentamerus* will probably show that some are representatives of *Pentameroides*. According to present information, this genus ranges from late Llandoverian through the Wenlockian.

Genus CONCHIDIUM Oehlert 1887

Conchidium munsteri St. Joseph 1938

Plate 40, fig. 3; text-fig. 4

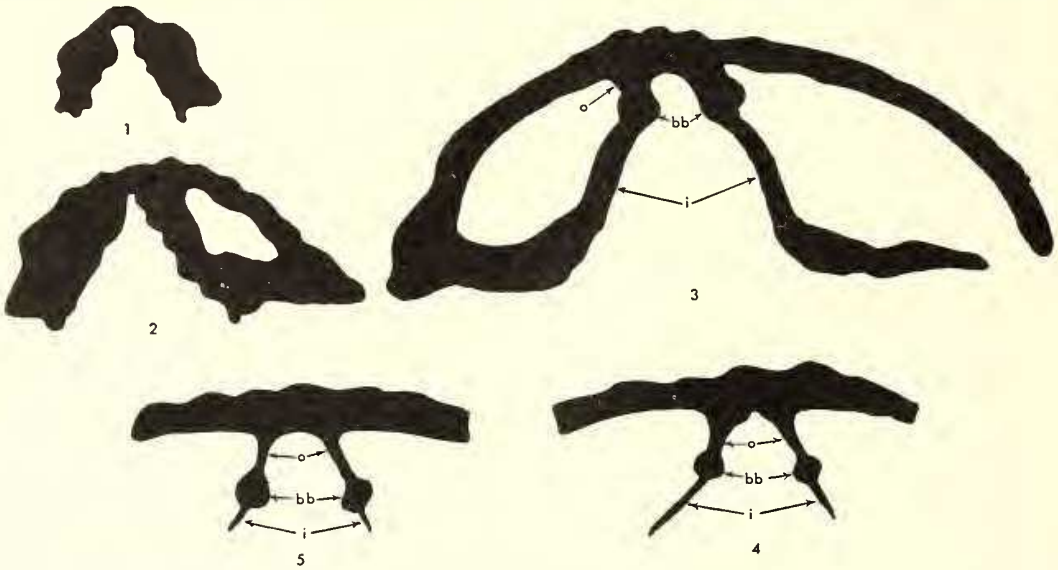
Conchidium munsteri St. Joseph, 1938, pp. 301–4, pl. 5, figs. 9, 11, pl. 6, figs. 10–11, text-figs. 7, 10.

Description. Elongate, biconvex shells without a well-defined fold and sulcus. They are moderately large, with fragmentary specimens suggesting a maximum length of between 40 and 50 mm. The pedicle beak is fairly prominent and the interareas appear to be poorly developed. Both valves are costate, four to five ribs occupying a space of 5 mm. The pedicle valve has a well-developed spondylium supported on a median septum which extends almost the complete length of the valve (St. Joseph, 1938, text-fig. 10, pl. 5, figs. 9, 11). In the brachial valve, the apparatus is tripartite with long, rod-like brachial processes supported on subparallel and discrete outer plates; on the valve illustrated in text-fig. 4, the outer plates extend forward at least 8 mm. The brachial processes are overlain by long inner plates.

Discussion. St. Joseph's description of this species was based upon pedicle valves from zone 5b in southern Norway. He noted that its stratigraphic position was unusual, being separated 'in time from the other representatives of this genus by the whole of the Llandoverian period', but concluded, on the basis of the internal and external character of the pedicle valve, that it was a true representative of *Conchidium*. In 1963 the writer borrowed a number of topotypes from the Palaeontological Museum at Oslo. This collection includes a number of brachial valves (no articulated specimens), three of which were serially sectioned, one being illustrated herein (Pl. 40, fig. 3; text-fig. 4). These show *C. munsteri* to have a well-developed brachial apparatus with long inner and outer plates. Its internal structure would seem to place it unmistakably in the subfamily Pentamerinae, and its external form relates it to *Conchidium*, or possibly *Rhipidium*. The specimens described by St. Joseph, and the pedicle valves observed by the writer, have

a fairly prominent pedicle beak, indicating that it is a representative of *Conchidium* rather than *Rhipidium*; however, no articulated shells have been observed, and the free pedicle valves observed by the writer are all at least partly embedded in matrix. It is, therefore, difficult to determine the lateral profile, especially the nature of the pedicle beak and umbo with respect to the brachial valve. Possibly a more definitive collection would show it to have the profile of *Rhipidium*.

The stratigraphic position of this species in zone 5b of Late Ordovician (Ashgillian) age is anamalous. Excluding *C. munsteri*, the oldest representative of the subfamily Pentamerinae comes from late Llandoverian strata; in fact, to the writer's knowledge,



TEXT-FIG. 4. Serial sections of the brachial apparatus of *Conchidium munsteri* St. Joseph, 1938. Zone 5b (Ashgillian), Vestre Svartoy, Ringerike, southern Norway. Drawings made from photomicrographs of parlodion peels; a photomicrograph of number 3 is shown on Plate 40, fig. 3. Distance from posterior tip of brachial valve: 1: 0·8 mm.; 2: 1·4 mm.; 3: 2·2 mm.; 4: 4·1 mm.; 5: 4·8 mm. (×5). On this specimen the outer plates extend forward at least 8 mm. Parlodion peels at the Paleon. Museum, Oslo, 16668A.

o—outer plate; bb—posterior extension of brachial process; i—inner plate.

there are no other Late Ordovician or early Llandoverian representatives of the entire family Pentameridae. However, according to information which Dr. Gunnar Henningsmoen kindly supplied to the writer there appears to be no reason to doubt that *C. munsteri* came from zone 5b. The only other Late Ordovician pentameracean is *Holorhynchus* which is also from zone 5b of Norway, but it is a representative of the Virgianidae with abbreviated brachial plates quite unlike the structure of *C. munsteri*. In this connexion it might be pointed out that Late Ordovician and early Llandoverian pentameraceans (with the exception of *C. munsteri*) appear to be confined to the families Virgianidae and Stricklandiidae, both of which are distinguished by their much abbreviated brachial apparatus. The family Parallelelasmatidae, which is believed to be confined to the Middle Ordovician, has a small pauciplicate shell quite unlike that of *C. munsteri*.

Subfamily GYPIDULINAE Schuchert and LeVene 1929[1]

This subfamily includes smooth, costate, pitted or granulose Pentameridae with fairly well-developed interareas. Generally they are strongly biconvex and many species develop a galeatiform shell. Most have a ventral fold and dorsal sulcus, but two genera (*Pentamerella* and *Barrandina*) have a ventral sulcus and dorsal fold, and a few have none. Commonly the shells are of small to moderate size, and only a few species have shells as large as the typical Pentamerinae. The brachial apparatus is well developed and may extend forward as much as half the length of the valve; it is tripartite and non-carinate, consisting of outer plates, brachial processes, and inner plates (text-fig. 1B). The outer plates may be parallel and discrete, or they may unite to form a cruralium.

In such typical genera as *Gypidula*, *Sieberella*, and *Pentamerella*, and probably in all the Gypidulinae, the processes are broad and blade-like. In *Sieberella roemeri* Hall and Clarke (1892, p. 242, pl. 2, fig. 6; Amsden, 1949, pp. 49–50, pl. 2, figs. 1–4; Amsden, 1951, p. 79, pl. 16, figs. 36–40), which is illustrated by photomicrographs on Plate 43, the processes are wide, nearly flat and have their ventral edges canted inward. These processes are supported on long outer plates, which are medially directed and overlain by inner plates which curve outward to meet the lateral edge of the valve; this plate arrangement produces the lyre-shaped cross-section which is so characteristic of the Gypidulinae (Pl. 40, figs. 5, 6, 9; text-fig. 5). Near the anterior end of the brachial apparatus, in the area where the brachial processes become free blades, the junction of the processes with the outer and inner plates may be detected in well-preserved sections (Pl. 43, figs. 4, 5). Further back, however, the plates lose their identity and are fused into what appears to be a single piece. Near the posterior end, in the area around the hinge, it is common for the entire brachial apparatus to be thickened by secondary shell material which serves to strengthen the articulating mechanism (Pl. 43, figs. 1–3). The gypidulinid structure is also well displayed in the etched brachial valve of *Gypidula coeymanensis* illustrated on Plate 40, fig. 5, 6. This is an unusually fine specimen, which shows the blade-like brachial processes and their relationship to the inner and outer plates. The structure is basically the same as that of *Clorindella* (Pl. 42, figs. 3–5) and other members of the Clorindinae, except that in the Clorindinae the brachial processes extend inside of the inner plates as carinae (text–fig. 1C). The external form of the Clorindinae is also similar to the Gypidulinae and the two subfamilies are believed to be closely related; in fact, until recently the genera which comprise the Clorindinae were included in the Gypidulinae. On the other hand, the brachial structure of *Sieberella* differs from that of *Pentamerus* and other members of the subfamily Pentamerinae which have slender processes that retain their identity well back towards the beak (Pl. 42, figs. 1, 2; Pl. 40, figs. 7, 8).

The subfamily Gypidulinae has been variously defined since it was introduced by Schuchert and LeVene in 1929. Schuchert and Cooper (1932, p. 171) used it for more or less galeatiform shells with small ventral interareas, and included six genera: *Clorinda* (*Barrandina* Booker, 1926 was regarded as a synonym), *Barrandella*, *Gypidula*, *Sieberella*, *Pentamerella*, and *Zdimir*.

Barrandella is a synonym of *Antirhynchonella*. In 1955 the International Commission on Zoological Nomenclature, Opinion 374, placed *Antirhynchonella* Oehlert, 1887 (type species *Atrypa linguifera* J. de C. Sowerby, 1839) on the *Official List of Generic Names in*

Zoology, and placed *Antirhynchonella* Quenstedt, 1871 (nomen nudum), and *Barrandella* Hall and Clarke, 1894, on the *Official Index of Rejected and Invalid Generic Names in Zoology*.

The writer would restrict the diagnosis of Schuchert and Cooper by removing genera like *Clorinda* and *Antirhynchonella* (= *Barrandella*), which have a carinate brachial apparatus to the subfamily Clorindinae. The group of shells which here comprise the Gypidulinae and Clorindinae were assigned by Nikiforova (1960, pp. 204–5) to two families: the Gypidulidae with discrete outer plates, and the Antirhynchonellidae with united outer plates. The writer does not believe this is a sound basis for distinguishing these two groups. The distinction between discrete and coalesced outer plates is not as sharply defined at the generic (or even specific) level as sometimes indicated, and in some species of *Sieberella* the outer plates may be separated slightly towards the front, and in some species of *Gypidula* these plates are almost joined. The type genus of Nikiforova's family Antirhynchonellidae is a representative of the Clorindinae, and therefore Antirhynchonellidae Nikiforova, 1960, should be suppressed as a synonym of Clorindinae (or Clorindidae) Rzhonsnitskaya, 1956. Rzhonsnitskaya (1961, p. 42) divided this group of pentamerids into two subfamilies: Gypidulinae, characterized by a ventral fold and dorsal sulcus and massive processes, and the Clorindinae with a ventral sulcus and dorsal fold and carinate brachial apparatus. The present writer assigns the uniplicate genus *Pentamerella* to the Gypidulinae because it does not have a carinate brachial apparatus, and this feature is believed to be of more fundamental importance than the position of the fold and sulcus. Actually, the development of a fold and sulcus in the Gypidulinae and Clorindinae is variable and some genera have none. Moreover, on some specimens belonging to species which normally develop a fold and sulcus this structure may be faint or absent.

The following genera are here assigned to the Gypidulinae: *Gypidula* Hall, 1867; *Barrandina* Booker, 1926 (see below); *?Biseptum* Khodalevich and Brievel, 1959 (may be a representative of the Pentamerinae); *Devonogypa* Havlicek, 1951; *Gypidulella* Khodalevich and Brievel, 1959, *Gypidulina* Rzhonsnitskaya, 1956 (synonym *Sieberina* Andronov, 1961); *Ivdelina* Andronov, 1961; *Leviconchidiella* Rzhonsnitskaya 1960; *Levigatella* Andronov, 1961; *Pentamerella* Hall, 1867 (see below); *?Procerulina* Andronov, 1961; *?Schegultania* Andronov, 1961 (no type species designated); *Sieberella* Oehlert, 1887; *Wyella* Khodalevich, 1931; *Zdimir* Barrande, 1881 (emended Boucot and Siehl). Most of these genera have a ventral fold and dorsal sulcus, but *Pentamerella* and *Barrandina* have a ventral sulcus and dorsal fold, and *Biseptum*, *Leviconchidiella*, and *Zdimir* generally lack a fold and sulcus. Representatives of this subfamily range from the Lower Silurian into the Upper Devonian.

Genus BARRANDINA Booker 1926

Barrandella (*Barrandina*) Booker, 1926, pp. 131–3.

Type species. *Pentamerus linguifera wilkinsoni* Etheridge, 1892, pp. 52–54, pl. 11, figs. 5–9. *Barrandella* (*Barrandina*) *wilkinsoni* (Etheridge). Booker, 1926, pp. 133–7, pl. 5, figs. 1–4, text-figs. 1, 2.

Discussion. Booker proposed *Barrandina* (as a subgenus of *Barrandella* Hall and Clarke 1894) for smooth, galeatiform shells having a ventral sulcus and dorsal fold. The pedicle

valve has a well-developed spondylium supported on a short septum. The brachial apparatus is tripartite, consisting of inner plates, brachial processes, and outer plates, the latter being subparallel and discrete; the brachial processes are blade-like. Booker treated *Barrandina* as a subgenus of *Barrandella* from which it was distinguished by an 'extra plate at the junction of the septa and crural plates'. As pointed out by Schuchert and Cooper (1932, p. 172), his 'extra plate' is only the brachial process which in *B. wilkinsoni* has a blade-like form (well shown in Booker's text-figs. 1, 2). These authors thought *Barrandina* had essentially the same external and internal structure as *Clorinda* and therefore suppressed Booker's subgenus as a synonym. In its smooth shell, pedicle sulcus and brachial fold, and discrete outer plates, *B. wilkinsoni* is similar to *Clorinda armata* (Barrande; type species). However, Booker's serial sections of *B. wilkinsoni* (figs. 1, 2) clearly show that the brachial processes butted smoothly against the inner plates, with no trace of carinae. In this respect it is unlike the carinate apparatus of *Clorinda* and other members of the Clorindinae. Accordingly, *Barrandina* is here regarded as a distinct genus and assigned to the Gypidulinae.

Booker described a second species, *B. minor*, in the same paper. His serial sections (figs. 3, 4) show the brachial apparatus to have an unusual doubly carinate structure. This is unlike any observed by the writer, and its relationship and significance are unknown. Booker (1926, p. 140, pl. 6, fig. 5, text-fig. 5) also redescribed *Pentamerella molongensis* Mitchell, 1920. This species has a smooth shell with a ventral sulcus and dorsal fold, a carinate brachial apparatus and discrete outer plates. This structure is typical for *Clorinda* and it is suggested that Mitchell's species be transferred to that genus.

B. wilkinsoni came from the 'Barrandella shales, Hatton's Corner, Yass', New South Wales. Booker did not assign an age to these strata, but Etheridge (1892, p. 54) correlated them with the Wenlock. The writer has no information bearing on this point.

Genus PENTAMERELLA Hall 1867

Pentamerella arata (Conrad) 1841

Plate 40, figs. 9–15; text-fig. 5

Atrypa arata Conrad, 1841, p. 55.

Pentamerus aratus (Conrad). Hall, 1857, pp. 120–1, figs. 1–8 [the pedicle valve shown in figs. 9 and 10 is probably a representative of *Conchidium*].

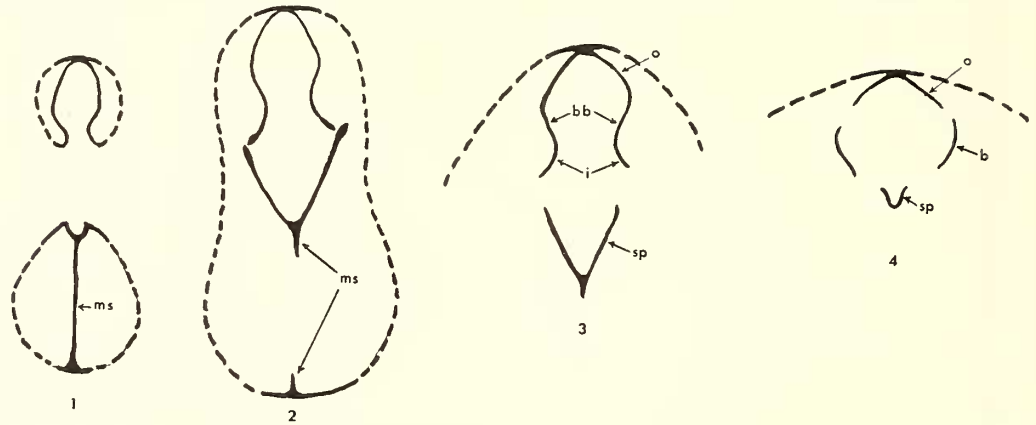
Pentamerella arata (Conrad). Hall, 1867, p. 375, pl. 58, figs. 1–10, 13–21 [the pedicle valve shown in figs. 9 and 10 is probably a representative of *Conchidium*]; Hall and Clarke, 1894, p. 71, figs. 21–29; Schuchert and Cooper, 1932, p. 176, pl. 26, fig. 20.

Description. This species has a biconvex shell with a swollen pedicle valve and a subgaleatiform profile. The width is about equal to the length; length/width ratio ranges from 0·9 to 1·1. All the specimens examined have a ventral sulcus and dorsal fold, but this varies considerably in its development. The fold and sulcus on specimens from the Schoharie Formation are clearly marked, although never deep (Pl. 40, figs. 12–14; Hall and Clarke, 1894, pl. 71, figs. 24–27); however, on some of Hall's type specimens from the 'upper Helderberg Limestone' (Onondaga Limestone), the fold and sulcus are deeper and better defined at the front (Pl. 40, figs. 10, 11, 15). The umbos of both valves are smooth or only faintly ribbed, but toward the front the shell develops strong

plications which commonly increase by bifurcation; three or four ribs occupy a space of 5 mm.

The specimen from the Schoharie Formation (Pl. 40, figs. 12–14) measures 13·4 mm. long, 14·3 mm. wide, and 10 mm. thick. The largest specimen in the Hall collections from the 'upper Helderberg Limestone' (Onondaga Limestone) of New York is 24·6 mm. long, 22·8 mm. wide, and 14·1 mm. thick. A complete shell from the 'upper Helderberg Limestone' at Waterloo, Iowa, measures 20·5 mm. long, 20·0 mm. wide, and 14·6 mm. thick.

The pedicle valve has a long, deep spondylium supported on a relatively short septum (text-fig. 5; Hall and Clarke, 1894, pl. 71, figs. 21, 22). The brachial apparatus is well



TEXT-FIG. 5. *Pentamerella arata* (Conrad). Transverse serial sections (×6) of one of Hall's unfigured paratypes from the Schoharie Formation (Lower Devonian), Albany Co., N.Y. (only the brachial apparatus is shown in figs. 3 and 4). Approximate distance from the posterior tip of ventral beak: 1: 0·5 mm.; 2: 2·1 mm.; 3: 3·0 mm.; 4: 3·9 mm. The parlodion peels from which these drawings were made are at the American Museum of Natural History, No. 2837/2.

b—brachial process; bb—posterior extension of brachial process; i—inner plate; o—outer plate; ms—median septum; sp—spondylium.

developed and extends forward almost half the length of the valve. The brachial processes are broad, blade-like structures braced by inner and outer plates, the latter uniting just at the valve floor to produce a cruralium (Pl. 40, fig. 9; text-fig. 5). Hall's unfigured paratype, which was serially sectioned, has a typical gypidulinid structure; the dorsal edge of the brachial process abuts against the ventral edge of the inner plate to produce a smooth junction with no trace of carinae. The silicified interior (Pl. 40, fig. 9) shows a low ridge at the posterior end of the cruralium, but this is the result of secondary shell deposition (common in mature pentamerid shells), accentuated by incomplete silicification at the posterior tip (compare Pl. 43, figs. 2, 3).

Discussion. Hall proposed the genus *Pentamerella* (type species *Atrypa arata* Conrad) for plicate pentamerids with a ventral sulcus and dorsal fold, and a cruralium. *Pentamerella* has generally been assigned to the Gypidulinae, but in 1956 Rzhonsnitskaya referred this genus to a new family, the Clorindidae, on the basis of its ventral sulcus and dorsal fold, and presumed carinate brachial apparatus. This last feature has never been

described in print and, in order to get precise information on its internal plate structure, the type species, *P. arata* (Conrad), has been restudied. Conrad's description of this species is believed to have been based upon specimens from the Schoharie Formation of New York. The writer has not examined Conrad's types, but, through the courtesy of Dr. Roger Batten of the American Museum of Natural History, he was able to study Hall's types (1867, pl. 71, figs. 11–21) which include specimens from the Schoharie Formation, Schoharie County, New York; the 'upper Helderberg Limestone' (Onondaga Limestone), the Helderbergs, Albany County, New York; the 'upper Helderberg Limestone' at the falls of the Ohio and at Waterloo, Iowa. Excluding one large pedicle valve from the Schoharie Formation (Hall, 1867, pl. 71, figs. 11, 12), which may be a species of *Conchidium*, these all appear to be congeneric. There is, however, some variation in the development of the fold and sulcus, and the specimens from the 'upper Helderberg Limestone' (Onondaga Limestone) of New York show a much stronger fold and sulcus than do the others. Whether this represents intraspecific variation or a distinct species cannot be determined without access to larger and more definitive collections. The internal structure can, however, be clearly determined on the basis of Hall's material. The silicified interior and the specimen sectioned, both of which are from the Schoharie Formation and presumably are topotypes, have a characteristic gypidulinid brachial structure with no trace of carinae. Accordingly the genus *Pentamerella* is here retained within the Gypidulinae.

Distribution. Conrad's specimens are believed to be from the Schoharie Formation of late Lower Devonian (Esopusian) age. Hall's collections include specimens from the 'upper Helderberg Limestone' (Onondaga Limestone) of New York, and the 'upper Helderberg Limestone' of Ohio and Iowa, although, as noted above, there is some question whether these are all conspecific. Oliver (1956, p. 1469) records *P. arata* from all four members of the Onondaga Limestone in New York.

The genus *Pentamerella* ranges from the Lower Devonian into the Upper Devonian. In 1953 (p. 143) the writer assigned the Silurian species *Barrandella areyi* Hall and Clarke to *Pentamerella*, but in the present report this species is made the type of a new genus, *Clorindella*.

Subfamily CLORINDINAE Rzhonsnitskaya 1956

This subfamily comprises small to medium sized, smooth to costate Pentameridae, with biconvex shells which tend to have a geleatiform profile. In the pedicle valve the spondylium and supporting septum are well developed. The brachial apparatus is also well developed and consists of inner plates, brachial processes, and outer plates. The inner plates, which are shorter than the outer plates, abut against the outside of the brachial processes, rather than against the upper or ventral edge of the processes; this causes the ventral edge of the processes to extend into the crural cavity as ridges or carina (text-fig. 1c; Pl. 42, figs. 3, 4).

The genera assigned to this subfamily are externally and internally similar to the Gypidulinae and, in fact, were until recently included in that subfamily. They are distinguished from the Gypidulinae primarily on the basis of their carinate brachial apparatus. This structure was first noted by Kozlowski (1929, p. 137, text-figs. 40, 41) in *Clorinda pseudolinguifera* Kozlowski and *Barrandella linguifera* (Sowerby) (*Antirhynchonella linguifera*). Kozlowski described it as a 'carena à la limite des plaques crurales